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ART. 9. LARVAL DEVELOPMENT OF *NECTOPHYRNOIDES*  
*TORNIERI* (ROUX), WITH COMMENTS ON DIRECT  
DEVELOPMENT IN FROGS

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(PLATES 1-3)

The African bufonid genus, *Nectophrynoides*, to which three species are now referred, comprises the only known ovoviviparous frogs. The two East African (Tanganyika Territory) species have long been known; *vivipara* was described by Tornier (1905), who referred it to the genus *Pseudophryne*, and *tornieri* was described and referred to *Nectophryne* by Roux (1906). Noble (1926) proposed a new genus, *Nectophrynoides*, for these two species, associating them principally because of their unusual mode of development. The third form, *occidentalis*, was described by Angel (1943), from Mt. Nimba in French Guinea, near the Liberian border.

The remarkable type of development of these frogs was discovered early, but until recently little detailed information on embryonic stages was available. Brief notes on embryos of *N. vivipara* were published by Tornier (1905) and of *N. tornieri* by Krefft (1911) and Noble (1927). Counts of uterine embryos were listed by Barbour and Loveridge (1928). The study of *occidentalis* by Angel and Lamotte (1944) is, however, the only detailed account of the development of these frogs that has come to my attention.

In the present paper, several stages in the early development of *tornieri* are described and compared with *occidentalis*, and some comments on direct development in relation to larval characters are presented.

*Acknowledgments.*—Through the courtesy of Mr. Arthur Loveridge and Mr. Benjamin Shreve of the Museum of Comparative Zoölogy I have had the opportunity to examine several series of embryos of *Nectophrynoides tornieri* in the MCZ collection. Preliminary study of this material was made in connection with my doctoral studies under the direction of Dr. Norman Hartweg, during tenure of a University Fellowship at the University of Michigan. Larvae in the University of Michigan Museum of Zoology (UMMZ) collection cited in this paper were also studied at that time. The *Nectophrynoides* material was re-examined in 1948. I am also indebted to Mr. Karl P. Schmidt for the recent opportunity to study

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larvae of *Rhinoderma darwini* in the collection of Chicago Natural History Museum (CNHM).

#### I. LARVAL DEVELOPMENT OF NECTOPHRYNOIDES TORNIERI

The material studied is divisible into five rather well-differentiated "stages" of development. Some are anatomically younger than the developmental stages of *N. occidentalis* described by Angel and Lamotte (1944), and provide more definite information on certain larval characters. My studies are not as detailed as those of Angel and Lamotte for I made no serial sections, determining internal characters only by simple microdissection.

The actual ages of the embryos are not known. In the numerical stage designations of the series, the term "stage" is used only to facilitate reference to particular specimens, and is not intended to have an exact morphological significance.

*First Stage.*—(Pl. 1, fig. 1) In this, the earliest stage available, the embryo is already well-formed; head structures are becoming differentiated, distinct limb bud anlagen are present, and there is a long thin tail. There is a large and rather ovoid (probably round in life) yolk mass. Unpigmented eye and ear capsules are visible, and the nasal pits are present. Jaw structures are still in a very rudimentary condition, and the mouth is not yet open. There is no external indication of adhesive organs. Two pairs of short but very distinct external gills are present. The front leg buds are still external. The long, thin, tail appears to be composed chiefly of notochordal tissue and very low, ridge-like, dorsal and ventral fins. Some of the specimens have a few faint melanophores on the body, but they are otherwise unpigmented. Total length  $\pm$  5.5 mm.

*Second Stage.*—(Pl. 1, fig. 2) The larvae of the second group are considerably advanced over the first series, particularly in the development of the head structures. The eyeballs are well differentiated and quite heavily pigmented. The mouth is a small, simple, transverse, slightly crescentic, opening. The opercular folds are of varying extent in different specimens and well illustrate the process of enclosure of the forelimb buds and formation of the spiracle. The morphological relations appear to be entirely as in a normal aquatic tadpole. In the least well-developed specimens the operculum already encloses the gill arch region and the base of the foreleg bud on each side, and forms a transverse fold entirely across the throat. In more advanced specimens fusion of the edge of the opercular fold with the body wall ventro-caudad to the foreleg buds is underway, forming an

opercular cavity and progressively reducing the size of its external opening (Pl. 2, figs. 1-4). The final step in this sequence of events is the refinement of the opercular opening remaining on the left side to form the spiracle. This is completed in specimens in the third stage (Pl. 2, fig. 5). In the gill region of specimens of the second stage, three small gill arches and two open gill slits can be seen. The first two arches each bear a single tiny gill rudiment. The leg buds are much better developed than in the first stage, and the tail is longer. There is a fine network of melanophores over the head and back. Total length  $\pm 6$  mm.

*Third Stage.*—(Pl. 1, fig. 3; MCZ 12513) The specimens in the third stage show further advances. Developmentally, they appear to agree most closely with Angel and Lamotte's Stage 1+ ("1 bis") of *N. occidentalis*. The eyes are very large and the facial region is small, embryonic in proportions. The small mouth shows definite though rather simple indications of larval structure. There are no beaks, labial teeth, or papillae, but there is a short fleshy ridge representing the larval lower lip. The sides of the upper jaw overhang the lateral part of the lower jaw (Pl. 3, fig. 1). The jaw region of one specimen was dissected, and it was found that the general pattern of the cartilages and muscles is essentially larval, although the proportions are, of course, much modified. The quadrate is shorter than in aquatic tadpoles, but a distinct processus muscularis is present. A small flat orbitohyoideus muscle connects it with the ceratohyal, which is of larval form and position. The other jaw muscles are more clearly shown in the fourth stage, and will be discussed in detail under that heading. Two pairs of open gill slits were found in the specimen dissected. There is a small but distinct spiracle on the left side. The dorsal surfaces of the head, body, and base of the tail, are finely speckled with melanophores. The leg buds are somewhat elongated, the posterior pair showing an indication of foot and leg segments. The tail is long and thin, with low rudiments of dorsal and ventral fins. Total length  $\pm 6$  mm.

*Fourth Stage.*—(Pl. 1, fig. 4; MCZ 12515) These larvae are approximately equivalent to Angel and Lamotte's Stage 2 of *N. occidentalis*. The general proportions are much the same as in the third stage, the principal changes visible externally being the larger and better developed legs and greater transparency of the skin. A very small sinistral spiracle is present; the nostrils are quite large; the mouth is still small. The legs and digits are well developed. The long rat-like tail has about 17 somites; the first 10-12 of them are well developed, the rest are rather irregular. The low, thin caudal fins are transparent and appear to contain an extensive vascular

network. The jaw region of one specimen was dissected (Pl. 3, figs. 2-4). The arrangement of the jaw cartilages and muscles was found to be essentially larval, as in the third stage, but the details were more easily worked out in the present specimen because of its somewhat larger size. The various structures are small and modified in proportions, in correlation with the embryonic contours of the entire head. The posterior part of the quadrate is quite short, the processus muscularis being not far anterior to the otic capsule. The processus muscularis is quite well differentiated although, as would be expected, its size relative to other cranial structures is much smaller than in aquatic tadpoles. The orbitohyoideus muscle is thin and transparent, and the underlying origins of the suspensorioangularis and ceratohyoangularis can be seen through it. The pterygoideus and the adductor mandibulae posterior longus have separate, laterally-adjacent origins, and the latter muscle appears to be differentiated into two slips distally, as in most aquatic tadpoles. Small adductor m. subexternus and articularis muscles are present, and have normal origins. All of the adductor muscles seem to insert on the lower jaw. In most aquatic tadpoles certain of these muscles insert on the upper labial cartilage, their insertions shifting to Meckel's cartilage during metamorphosis. A narrow strap-like subhyoideus muscle and a thin crescent-shaped intermandibularis are present in the normal larval positions. The lower jaw is differentiated into the typical Meckelian and lower labial segments, but histological studies will be needed to determine whether these cartilages are separate or fused, and whether there is a distinct upper labial cartilage. The specimen dissected appeared to have three open gill slits on each side. On the left side, the first gill arch was larger than the others and bore two rows of minute gill rudiments; on the right side the first two gill arches were of approximately equal size and bore no distinct traces of gills. A typical larva in this series has a total length of 10 mm., head and body length 4 mm.

*Fifth Stage.*—(Pl. 1, fig. 5; MCZ 12512) In this series, metamorphosis is well underway and the specimens are approximately in Angel and Lamotte's Stage 3 of *occidentalis*. The forelegs have emerged; anterior to each a small slit remains, connecting the gill arch region with the outside. The head proportions are still embryonic, with relatively huge eyes, but the mouth has begun to enlarge. The rudimentary lower lip has disappeared. The long, thin, rat-like tail is still present. The hind legs show traces of dark banding, but the body is still rather weakly pigmented. The total length at this stage is  $\pm$  11 mm., snout-vent length  $\pm$  4.5 mm.

## DISCUSSION

It is instructive to re-assemble the notes on external characters in the form of a routine diagnosis so the larval stage of *N. tornieri* can be more easily compared with conventional tadpoles: Head and body narrow; head small; facial region of embryonic proportions, with very small jaws; eyes very large. Spiracle very small and inconspicuous, sinistral. Tail long, thin, rat-like in proportions, consists principally of a well-developed notochord partly concealed by about 17 small somites basally and with very low ridge-like dorsal and ventral fins. Mouthparts greatly simplified; mouth very small, jaws devoid of horny beaks, with or without a short flap-like rudiment of lower lip; no tooth ridges, labial teeth, or papillae. Dorsum weakly pigmented with fine network of melanophores. Tail colorless or with a few scattered melanophores basally. Maximum total length before metamorphosis  $\pm 11$  mm.

Although *tornieri* is ovoviviparous and undergoes direct development, it is evident that few of the important characters of the tadpole stage have actually been lost. There is no external indication of adhesive organs, labial teeth, or horny beaks in the material studied. Anatomically, these structures are relatively superficial, and they are commonly lost in species that undergo direct development or other modifications of the life history. On the other hand, *tornieri* has a distinct trace of a larval lower lip (at least in some specimens), the internal structure of the jaw region is essentially larval in pattern, a spiracle is present and its development is essentially typical. Tiny but distinct gill arches, gill slits, and external gills develop. Although the general proportions of the head, body, and tail have become greatly modified, it is clear that this species still retains the more fundamental characters of the tadpole stage in recognizable condition and still undergoes an extensive metamorphosis. Anatomically, there is a well-defined tadpole stage even though it is no longer free-living.

Angel and Lamotte emphasized the absence of a spiracle in *N. occidentalis*. From the figures and description of their Stages 1 and 2, however, it is obvious that opercular folds develop in that species, for the foreleg buds are internal. During the growth of the operculum in the period preceding their Stage 1, a spiracle would therefore have been present, although it may subsequently have closed completely. Developmentally, the spiracle of the tadpole is merely the excurrent opening remaining after most of the free margin of the opercular fold has fused with the body wall below and behind the gill region. The size of the spiracle depends on how complete this fusion is; the more complete the fusion, the smaller the

spiracle. It is possible that vestiges of gill arches and associated structures will also be found in younger embryos of *occidentalis* when such specimens become available. The internal structure of the jaw region of embryonic *occidentalis* is not yet known. It will be of considerable interest to learn how much (if any) of the larval arrangement of cartilages and jaw muscles is still retained in that species. Angel and Lamotte reported no indication of any external buccal structures.

Angel and Lamotte noted that in the stages of *occidentalis* available to them the ovarian eggs are very minute (diameter 0.2 mm.), and there is no trace of a large yolk mass in the embryo. Although there is a wide developmental gap between the ovarian egg with a diameter of 0.2 mm. and an advanced embryo with a total length of 4.5 mm., the next stage available to them, they concluded that the egg remains poorly equipped with yolk and that virtually all nourishment must therefore be provided through maternal tissues. Description of the intervening stages (the mature ovum and pregastrular phases of embryonic differentiation) in this species will be awaited with great interest.

## II. COMMENTS ON DIRECT DEVELOPMENT IN FROGS

In recent years there has been an increasing interest in problems relating to direct development in frogs. Lutz (1947, 1948) has reviewed the general field, with particular reference to the complex frog fauna of southeastern Brazil. She emphasized, among other points, the extensive parallelism shown in various unrelated groups of frogs that have independently achieved specialized developmental patterns, and the tendency for non-functional larval structures to be reduced or entirely lost in non-aquatic types of larvae that have an increased yolk supply. These trends result in a more or less direct transition from generalized embryo to frog without the intervention of a specialized free-swimming larval stage.

The fate of larval structures in non-aquatic development differs widely among different species, and various degrees of retrogression of these structures can be demonstrated. In a typical aquatic life history, critical early phases in the formation of tadpole structures are completed so rapidly and at such a small larval size that they are difficult to study. In the comparatively larger embryos of non-aquatic forms, these early phases (especially in the jaw and branchial regions) are prolonged and the relative growth rates are altered, with the result that the structural relations are somewhat clarified. Some of the problems in tadpole anatomy on which this situation affords evidence are discussed below.

## 1. THE TADPOLE OPERCULUM AND SPIRACLE

The anatomical relations of the operculum and spiracle to the underlying structures in the tadpole are complex, but can be better understood by comparing the developmental sequence in typical aquatic tadpoles with that in various specialized non-aquatic frog embryos. The so-called operculum of the typical tadpole has a dual origin. It is derived principally from the transverse dermal fold growing backward from the hyoid region, but a low ridge-like fold across the anterior part of the belly is incorporated into the completed structure. The latter fold develops posterior to the level of the foreleg region and extends vertically to a point above it, so that the fusion of the two components of the operculum encloses not only the gill chamber, but with it the area in which the foreleg will develop. Ordinarily, the process is carried to completion, leaving only a small excurrent opening, the spiracle. In frogs with an abbreviated larval history, the development of the operculum and spiracle may remain fairly typical or it may be arrested at some point short of completion. The process is completed in *Nectophrynoides tornieri* (Pl. 2, figs. 1-5), *Rhinoderma darwini*, *Pipa aspersa*, and *Pipa pipa*; in the latter two forms, symmetrically paired spiracles develop, as in aquatic larvae of other Pipidae and of *Rhinophrynus*.

In certain forms in which the operculum remains incomplete, the homology of the dermal vestiges in the branchial region has been questioned. Lynn (1942) suggested that the small dermal fold over the base of the foreleg bud in *Eleutherodactylus* embryos is not homologous with the operculum of the typical aquatic tadpole. In various forms of *Gastrotheca* and related genera of "marsupial" hylids, a graded series of departures from the complete pattern of opercular formation can be demonstrated, and these help to interpret conditions in *Eleutherodactylus*. As is now well known from the work of Noble (1927) and others, some marsupial hylids have an aquatic larval stage and others have direct development, but in all known forms the young are carried on the back of the female during at least the early phases of development. All, so far as known, have the same highly diagnostic peltate (*cf.*, nasturtium leaf) type of external gills, which form a thin vascular sheet enveloping the embryo. Because of the comparatively large size attained by these embryos and the relatively slow (apparently) completion of branchial development, they are excellent material for the study of operculum formation. Several series of embryos of *Gastrotheca* sp. examined (*e.g.*, UMMZ 68165) were found to have larval body and tail proportions and buccal apparatus and to have dis-

tinct leg buds before operculum formation was completed. The long-delayed closure of the operculum in these larvae is evidently associated with prolonged functioning of the relatively huge peltate external gills. In these large pre-hatching larvae, the composite origin of the operculum and its relation to the gill arches and to the already well-formed foreleg buds are very clearly shown.

In the exceptionally large embryos of *Hemiphractus divaricatus* (UMMZ 92106), the various structures are much modified in proportions and somewhat displaced by the relatively huge yolk mass (its diameter  $\pm$  10 mm.). In the stage studied, there is a short, rather thick, flap-like fold across the throat and overlapping the bases of the long gill stalks; laterally the fold thins out somewhat and forms a deep pocket surrounding the base of each foreleg bud. The structural relations here, although much altered in proportions, are not basically different from conditions in the young pre-swimming larvae of *Gastrotheca* described above. The developmental sequence in the series of *Gastrotheca* is in turn only proportionately different from that of an ordinary tadpole with a typical larval history. The differences are in degree only; the structures involved are the same in each of these forms.

In embryos of *Eleutherodactylus cooki* (UMMZ 73550), the presence of a short dermal fold over the base of the foreleg bud and the absence of a transverse opercular fold across the throat were observed, as described by Lynn (1942) and other authors for other species in this genus. Morphologically, this condition appears to be but a further simplification of the opercular pattern noted above for *Hemiphractus divaricatus*. The transverse part of the composite operculum has become entirely suppressed and all that remains is the pocket-like fold over the base of the foreleg anlage. If the composite origin of the tadpole operculum is granted, it is probable that the dermal fold over the foreleg bud in *Eleutherodactylus* is homologous with the postero-lateral part that normally encloses the foreleg within the gill chamber, and thus the fold may be correctly interpreted as an opercular vestige.

As noted above, the spiracle is not always formed in non-aquatic frog embryos. Theoretically, it could be eliminated from the phenotype either by complete closure of the opercular folds, or by their failure to close at all, leaving a wide gap through which the branchial region and foreleg buds remain exposed. Examples of the latter type include *Eleutherodactylus* and *Hemiphractus*. In such forms the forelegs are more or less fully visible externally throughout their development. Absence of a spiracle



as the result of complete opercular closure has been reported in *Sooglossus* (Brauer, 1898), *Breviceps* (de Villiers, 1929 a), *Anhydrophryne* (Hewitt, 1929), and *Arthroleptella* (Power and Rose, 1929; de Villiers, 1929 b), and has been tentatively suggested for *Zachaenus parvulus* by Lutz (1944). In *Nectophrynoides tornieri* and *Rhinoderma darwini* the spiracle is so small and inconspicuous that high magnification and careful handling are required in order to locate it. Consequently, it is suggested that a spiracle may prove to be present in some of the forms listed above.

## 2. MODIFICATION OF THE MOUTHPARTS

The mouthparts of frog tadpoles are a highly complex mechanism that has undergone many remarkable evolutionary changes. In species having non-aquatic development, there is a trend toward loss of the typical larval buccal structures (*vide* Lutz, 1948), but the degree to which this has been accomplished differs widely between different species. Study of these modified types of mouthparts suggests not only some features relating to sequence of loss of structures, but also some possible clues to the origin of certain parts of the buccal apparatus.

In the simplification of the mouthparts in non-aquatic larvae, the end result may be structurally similar in forms having no close taxonomic affinity. That similarity should, however, be interpreted with reference to the type of larval mouthparts occurring in related free-swimming tadpoles. For example, the absence of beaks and labial teeth in embryos of *Pipa pipa* does not necessarily mean that they have been secondarily lost in the course of modifying the life history of this species, for these structures are likewise absent from all known free-swimming pipid tadpoles. Similarly, beaks and labial teeth are not known to occur in aquatic larvae of the Microhylidae, and would therefore not be expected in terrestrial embryos of microhylids.

Loss of the labial teeth in relation to direct development involves both the disappearance of the rows of pigmented labial teeth themselves and the tooth ridges upon which they are borne. Histologically, the teeth, and probably also the beaks, may remain after there is no longer any readily observable external indication of their presence. Noble (1927) figured and discussed the small non-horny labial tooth remnants revealed in sections through the lip of larval *Rhinoderma darwini*. The jaws of *Rhinoderma* are typically larval in form and proportions. They tend to be sheathed with an opaque white layer which, although not hardened, is visually different from adjacent surfaces. The internal jaw structures of *Rhinoderma*

have not yet been described. The head contours are typically larval, however, especially the region of the processus muscularis of the quadrate and the orbitohyoideus muscle, as can be seen through the partly transparent skin (CNHM 3684).

In non-aquatic embryos in which the beaks and labial teeth are no longer externally apparent, more or less well-defined traces of the larval lips may still remain. *Rhinoderma darwinii* (CNHM 3684) has nearly typical lips with normal marginal papillae, and across the lower lip are either two or three papillose, fringe-like, remnants of labial tooth ridges. In *Hemiphractus divaricatus* (UMMZ 92106), the original larval lips are reduced to a narrow papilla-edged labial fold along the sides of the upper jaw and continuing along the base of the lower jaw for a varying distance, reaching the symphysis in some specimens. In this form the upper jaw is greatly simplified. The small lateral papillae are borne directly on the edge, the separate dermal margin (upper lip) having been lost. In a series of embryos of *Cryptobatrachus fuhrmanni* (UMMZ 47409), a still further reduction is found, and all that remains of the external mouthparts is a very short labial fold bearing a few papillae laterally and none at all on its very low median continuation along the lower jaw. Morphologically, this is a further step in the trend toward reduction of the mouthparts shown by *Hemiphractus divaricatus*.

In *Nectophrynooides tornieri* the maximum development of external mouthparts in the material examined is shown in specimens (MCZ 12513) having a short fleshy fold along the base of the lower jaw, clearly a vestige of the lower lip of typical aquatic tadpoles (Pl. 3, fig. 1). It is not equally well developed in all specimens in this series, and is probably both transient in the individual and of variable occurrence in the species. In *Eleutherodactylus* this morphological trend has apparently reached its logical conclusion, for no larval lip structure has been demonstrated in this genus (see especially Lynn, 1942). It is probable, however, that the peculiar horny egg tooth in *Eleutherodactylus* embryos is a specialized derivative of the upper beak of a typical aquatic tadpole, judging from its position and from Lynn's (1942) note on its histological structure in *E. nubicola*.

The greatly reduced lip rudiments in embryos such as *Hemiphractus* are structurally much like the simple labial folds of pipid tadpoles. In these tadpoles, in turn, there is a close resemblance to the type of labial folds characterizing salamander larvae and many of the fishes. At this point, the factual basis for comparison becomes rather tenuous, but the temptation cannot be resisted to suggest that the origin of the complex

lips of the specialized aquatic tadpole can be traced to the simple lateral labial folds that are of such widespread occurrence among the lower vertebrates. The convergent development of complex lips in certain South American catfishes and stream-dwelling Asiatic cyprinids provides supporting evidence of a possible homology of these structures in amphibians and fishes. Young larvae of the Australian lungfish possess labial folds very similar in form and position to those of salamander larvae.

Very little has been published on the internal anatomy of the jaw region of non-aquatic larvae, but the scant published data that I have found, together with the brief exploratory studies made during my doctoral research at Michigan, suggest that in these specialized forms the cartilages and muscles of the jaw region tend to become simplified. This would, of course, be expected, in view of the reduction of other larval structures in direct development. In some forms the jaw pattern is essentially that of a typical tadpole. The general trend towards simplification seems to include the following features: basal part of the quadrate shortens, returning the suspensorium to more nearly the adult position (*Cryptobatrachus*, *Nectophrynoides*); Meckelian and lower labial cartilages lose their movable articulation with each other and become a more or less continuous band of cartilage (*Cryptobatrachus*, *Nectophrynoides*); the upper labial cartilage is reduced in size and distinctness, and eventually becomes indistinguishable from the general cartilage field of the trabecular region; the quadrato-cranial commissure fails to develop in some forms, including *Eleutherodactylus nubicola* (Lynn, 1942); the processus muscularis of the quadrate becomes greatly reduced in size but, with its orbitohyoideus muscle, it tends to retain a typically larval appearance (e.g., in *Pipa pipa*, *Cryptobatrachus fuhrmanni*, *Nectophrynoides tornieri*); it is absent in *Eleutherodactylus nubicola*.

Suppression of larval characters is more nearly complete in *Eleutherodactylus* than in any other frogs with non-aquatic development that have been reported thus far. Closely related genera that are known or suspected to have non-aquatic larvae, especially *Syrrophus*, *Tomodactylus*, and *Microbatrachylus*, should provide valuable comparative data when their early stages are discovered.

The occurrence of direct development in frogs of very diverse taxonomic relationships indicates that it is not a single phylogenetic trend, but rather is a general tendency that has evolved independently in unrelated stocks. Thus far it is known in a relatively small number of species, but these are

distributed through 10 of the 13 families<sup>1</sup> that are currently considered valid.

It is worthy of emphasis that among tadpoles there is evidence of evolutionary trends of opposite nature. In one direction is the important general tendency toward elimination of the tadpole stage through direct development, while in the opposite direction is the widespread tendency toward ever greater complexity of the tadpole stage, as in the extremely specialized larvae of *Hyla claresignata*, *Rana rugulosa*, *Staurois*, and many others. Although this is on a small taxonomic scale (a single order), it appears to be an excellent example of the random nature of evolutionary trends.

#### SUMMARY AND CONCLUSIONS

Several early stages in the development of the ovoviviparous frog, *Nectophrynoides tornieri*, are briefly described and compared with similar stages of *N. occidentalis* reported by Angel and Lamotte (1944). Although the embryos of *tornieri* are highly modified in many respects, they develop numerous tadpole characters, and in their structural plan as a whole they are definitely larval. Small external gills, gill arches, and gill slits develop; typical opercular folds form and enclose the gill region and foreleg anlagen; a spiracle develops; a rudimentary lower lip is present, at least in some specimens; and there is a typical larval arrangement of internal jaw structures. Other details of body and tail structure are also mentioned.

Discrepancies between larval characters of *tornieri* reported here and those of *occidentalis* described by Angel and Lamotte (1944) are at least in part due simply to the availability of earlier stages of the former species, in which the development of the jaw and branchial regions can be more clearly traced. The internal position of the forelegs in *occidentalis* indicates that in this species, as in *tornieri*, larval opercular folds and at least a transitory spiracle develop.

The problem of direct development in frogs is discussed, with a detailed account of modifications of the operculum and spiracle and the mouthparts in non-aquatic larvae. The process of opercular development and spiracle formation is compared in typical aquatic tadpoles and in embryos of forms with direct development. It is concluded that the structures concerned and their anatomical relations are the same in both

<sup>1</sup> Examples known in Pipidae, Microhylidae, Ascaphidae, Pelobatidae, Lep-  
todactylidae, Bufonidae, Atelopodidae (*Rhinoderma*), Dendrobatidae (*Sminthillus*),  
Hylidae, and Ranidae; probably occurs in some Rhacophoridae; unknown in  
Rhinophrynidae and Discoglossidae.

life history types. Successively more simplified departures from the typical process are traced in several species having direct development, including *Nectophrynooides tornieri*, *Gastrotheca* sp., *Cryptobatrachus fuhrmanni*, *Hemiphractus divaricatus*, and *Eleutherodactylus* sp. When these forms are studied in morphological sequence, it is seen that they conform to a common developmental pattern. The complex dual origin of the tadpole operculum is discussed; the dermal fold above the foreleg bud in *Eleutherodactylus* is considered to be a remnant of the postero-lateral, non-hyoidean, part of the composite operculum.

In the non-aquatic larvae of frogs with direct development, there is a tendency toward simplification of the mouthparts. The beaks and labial teeth fail to harden or to form pigment, and eventually fail to develop at all; the lips and papillae are small and of simplified structure, and in extreme cases become reduced to narrow labial folds. The internal parts of the jaw apparatus tend to retain a larval pattern after the external structures have been lost, but even the jaw cartilages and muscles may by-pass the larval plan (as in *Eleutherodactylus*). It is suggested that the horny egg tooth of *Eleutherodactylus* was probably derived from the upper beak of the aquatic tadpole.

Comparison is made between the basic lip structure of tadpoles and the closely similar labial folds of salamander larvae and certain fishes, and it is suggested that these structures are probably homologous.

In direct development, the tadpole may be entirely lost ecologically, but a substantial part of the larval structural pattern usually develops. Thus, a tadpole stage, with a more or less extensive metamorphosis, is still present anatomically even though all outward evidence of it disappears before hatching occurs.

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## EXPLANATION OF PLATE 1

Several stages in larval development of  
*Nectophrynooides tornieri* (lateral views).

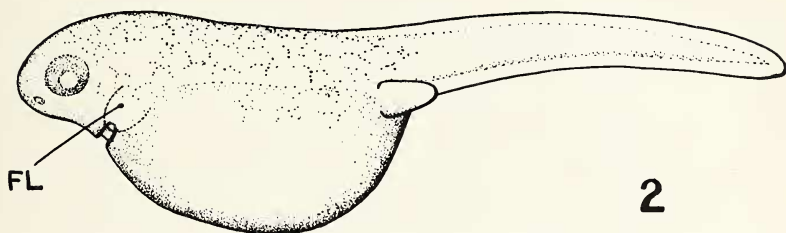
- FIG. 1. "Stage 1." Total length  $\pm$  5.5 mm. Small external gills present; operculum not yet distinct; foreleg bud external.
- FIG. 2. "Stage 2." Total length  $\pm$  6 mm. Operculum well developed, partly encloses foreleg bud.
- FIG. 3. "Stage 3." Total length  $\pm$  6 mm. Spiracle formation completed, foreleg bud internal.
- FIG. 4. "Stage 4." Total length 10 mm. Front leg visible through thin skin of closed operculum.
- FIG. 5. "Stage 5." Total length  $\pm$  11 mm. Metamorphosis has begun; front leg has emerged from opercular cavity; mouth enlarging.

EG, external gill; FL, front leg; S, spiracle.

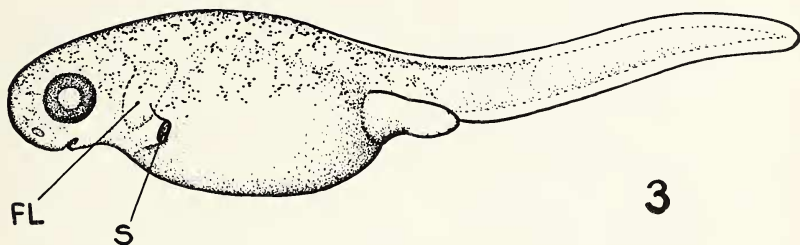




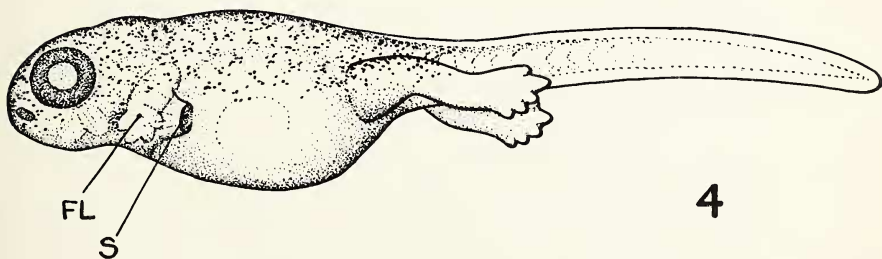
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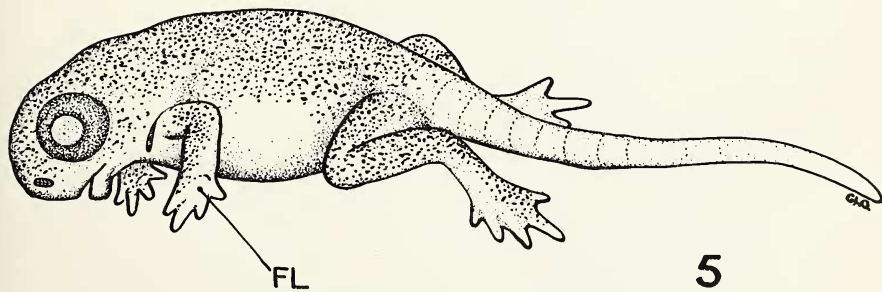
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